POPULATION STRUCTURE, SEASONALITY, AND HABITAT USE BY THE GREEN LYNX SPIDER *PEUCETIA VIRIDANS* (OXYOPIDAE) INHABITING *CNIDOSCOLUS ACONITIFOLIUS* (EUPHORBIACEAE)

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ABSTRACT. For one year we studied the habitat use of *Peucetia viridans* living on *Cnidoscolus aconitifolius*, in a pasture land in Mérida, Yucatán, México. Highest spider density was recorded in August (total 118, adults 77), and lowest in May (total 7, adults 2). Spider density was significantly higher in isolated plants and lower in plants in a patch. Sex ratio ($\female$:$\male$) varied from 1:1.5 in April, to 1:1 in May, and to 1:0.1 in September. The dominant instar (both sexes) changed during the study. Throughout the study more spiders were recorded in 'repose' than performing any other activity. Foraging and feeding were more intense between July and September, when their prey, flower visitors, were more abundant. The number of spiders on plants varied spatially and temporally due to the combined effects of distance of the individual plant to the nearby forest, monthly precipitation, plant height, and number of panicles in anthesis. Forty-eight percent of the spiders were found living on plants with 20–30 panicles in anthesis (2% of the plant population). Most of the spiders (except for adult females) were found either below or above leaves. There were no significant differences in the distribution of most stadia respective to plant height. Positive significant correlations were found between the number of spiders and the abundance of floral visitors when the data were compared shifted-back one month, and between the number of spiders and the number of panicles in bloom when the data were compared shifted-back two months. When the abundance of spiders, floral visitors and number of panicles in bloom were correlated to monthly precipitation, we found a positive significant correlation for spider abundance when the data were compared shifted-back three months, a significant negative correlation for floral visitors when the data were compared shifted-back two months, and a nonsignificant correlation for the number of panicles in bloom, although both (panicles and floral visitors) peaked in May.

Keywords: *Peucetia viridans*, *Cnidoscolus aconitifolius*, population structure, seasonality

Animals which are mobile during a period of their life actively select a site for nesting, feeding and reproduction. The latter may be influenced by parental habitat occupation, high density of competitors, or habitat availability at certain times of the year. The new site has to provide enough food, adequate nesting conditions, and protection against enemies and adverse weather conditions. Food resources are patchily distributed for most animals, regulating their feeding behavior, population dynamics, fitness and ultimately their evolution (Bronstein 1995). Thus, the fitness of an animal should be directly influenced by its ability to find a suitable habitat, which is based on an innate preference for certain high-quality environmental characteristics (e.g., absence of enemies and availability of food and shelter). Object organization in space is used to locate such habitats (McCoy & Bell 1991). Environmental characteristics exert a strong influence on habitat selection in spiders (Uetz 1991). For example, spiders depend on the structure of the environment because: (1) they need attachment sites for their webs, and (2) their sensory organs are based on the recognition of tactile vibrations of the substrate (Rovner & Barth 1981; Uetz & Stratton 1982). Spider populations show certain associations between their structure and the heterogeneity and/or structural complexity of the plant community (Chew 1961; Riechert &

Reeder 1970). Certain spiders have highly specific associations with plants. Thus their abundance and richness depend directly on the availability of specific plant species. The association between spiders and plant community structure suggests stratification of species or habitat partitioning, which should decrease interspecific competition. Spiders select sites based on the level of protection against extreme temperatures and the destruction of webs and nests, maximizing foraging time on the web. Similarly, they use environmental elements as indicators of prey availability, e.g., plant flowering (Morse 1984; Pollard et al. 1995).

Our field observations in the Yucatán Peninsula, México, have shown a close association between the green lynx spider (*Peucetia viridans* Hentz, Oxyopidae) and *Cnidoscolus aconitifolius* (Mill.) I.M. Johnstone (Euphorbiaceae). However, the characteristics that determine this habitat selection are largely unknown. The purpose of this research was to describe quantitatively this spider-plant interaction, and to explain the physical and spatial characteristics of the habitat used by the spider. In particular, we addressed the following questions: (1) Which plant parts does the spider use more frequently? (2) Which plant characteristics determine the presence of the spider? (3) Are all the stages in the life cycle of the spider accomplished on *C. aconitifolius*? (4) How does the population of the spider vary through time? and (5) Is there synchrony between the flowering time of the plant and the life cycle of the spider?

METHODS

Study site and organisms.—Field work was conducted in a 13,000 m² grassland owned by Universidad Autónoma de Yucatán, located 15.5 km south of Mérida, Yucatán, México (20°58′N, 89°37′W, elevation 9 m), which is surrounded on three sides by grassland, and on one by tropical lowland dry forest (canopy height is ca. 15 m).

The genus *Cnidoscolus* is characterized by the presence of urticant compounds which contribute to plant defense against herbivores (Harborne & Turner 1984). *Cnidoscolus aconitifolius* has extrafloral nectaries which are visited by ants, flies, bees and wasps. The inflorescence is a panicle with feminine and hermaphroditic flowers (both flowers may be pre-

sent in one panicle) and has no specific pollinators (Carbajal-Rodríguez 1998). In the study site, *C. aconitifolius* is distributed in clumps of up to 12 individuals, but solitary individuals are common.

The green lynx spider (*Peucetia viridans*) is a cursorial hunting spider, foraging by day and night on a wide variety of prey, commonly living on wild flowers, grasses, low shrubs or weeds (Whitcomb & Eason 1967; Nyffeler et al. 1987a, b, 1992; Weems & Whitcomb 1977; Simon 1980; Van Niekerk & Dippenaar-Schoeman 1994; Whitcomb et al. 1966). It is the dominant polyphagous predatory arthropod in certain systems. Its diet includes several insect orders, spiders (including its own species), and at times it preys on individuals up to 2.5 times larger than itself (Nyffeler et al. 1988a, 1992). In Texas and Florida, *P. viridans* is frequently associated with *Croton capitatus* (Euphorbiaceae), and with related genera like *Gossypium* (Malvaceae) and *Helianthus* (Asteraceae), where it plays an important role as predator of noxious fauna (Randall 1982; Simpson 1995). *Peucetia viridans* is considered an annual univoltine species, with a reproductive season during the summer. Oviposition (25–600 eggs) is during the autumn, hatching and dispersal of juveniles by ballooning takes place during the winter; and growth of juveniles takes place in spring (Exline & Whitcomb 1965; Whitcomb & Eason 1965).

Sampling design and statistics.—Field observations were made between April and September of 1997 during the last 10 days of each month; a typical day started at 0800 h and finished at 1300 h. In the first visit we marked all *Cnidoscolus aconitifolius* individuals ($n = 183$) in the sampling site. For each plant we recorded height, cover (see below), number of panicles in anthesis, distance to the forested area, and their aggregation pattern (i.e., whether isolated or in a patch, see below). To estimate plant cover, we used the formula for an ellipse ($C = 0.25\pi D_1 D_2$, where D_1 and D_2 are two perpendicular diameters crossing the center of the plant) rather than a circle, because *C. aconitifolius* shrubs are quite irregular and fit better an oval shape. A plant was considered in a patch when its leaves overlapped with another individual and/or the distance between the base of their stems was no more than 40 cm; if these parameters were not

met the plant was considered as solitary. The distance to the forested area was considered important because (1) it is probably the source of young spiders colonizing *C. aconitifolius* individuals in the grasssland, and (2) because environmental conditions are different closer to the forest (e.g., more shade and humidity, and less insolation).

On each visit we counted all *Peucetia viridans* individuals present per plant, and for each spider recorded: sex, activity (repose, foraging, feeding, care of offspring or egg sacs, courtship), location on the plant (on the stem, above or below a leaf, among new leaves, among the inflorescence, on a panicle), height above the ground, and size. To estimate size we used the width of the cephalothorax, which is relatively fixed per developing instars (nine instars for females, and eight for males) (Brady 1964; Killebrew & Ford 1985; Louda 1982; Randall 1978; Van Niekerk & Dippenaar-Schoeman 1994; Whitcomb et al. 1966). To accomplish the above, spiders were not removed from the plants. Instars were estimated using previously collected and measured individuals, which were organized by size in a cotton-stuffed vial and preserved in 70% alcohol. The vial was placed near a spider and size was established by comparison.

We estimated the abundance of floral visitors per month using five inflorescences on each of 10 isolated and 10 grouped individuals randomly selected. All visitors were counted when they made physical contact with the flowers at the time of peak activity (1200–1230 h). A three-way analysis of variance (SigmaStat 1995) was used to determine differences on the abundance of floral visitors among months and between isolated and grouped plants; the data was transformed by obtaining the square root of the value plus one (Zar 1996). We used a two-way analysis of variance (SigmaStat 1995) to determine if *P. viridans* exhibits (1) vertical stratification on the plant, (2) location preferences among instars and over time, (3) changes on activity intensity over time, and (4) comparison of spider abundance per plant grouping over time. A log-linear model was fitted with the GLIM-4 statistical system package (Francis et al. 1993) to test the hypothesis that spider presence is correlated to plant characteristics (number of panicles), and that synchrony exists between plant phenology, the life cycle of

the spider (abundance and instar-structure per month), and the precipitation pattern of the study site. Because we used "count data," the goodness-of-fit was evaluated with a χ^2 test using the G statistic and a Poisson error distribution. With Poisson errors, the change in variance can be compared directly with χ^2 tables to assess its significance (Crawley 1993).

In order to estimate the synchrony between plant phenology and the life cycle of the spider, we compared the number of blooming panicles of *Cnidoscolus* and the number of floral visitors to the abundance of *Peucetia* per month. As organisms usually need time to respond to changes in their environment (e.g., Ogata et al. 1996), these correlations (Pearson) were computed following a time lag scheme, which consisted in taking the resultant spider abundances for a specific month and correlating them with the blooming panicles and/or floral visitors abundances of the preceding months. Correlations were computed at one, two and three months time lag.

RESULTS

Population parameters.—Highest spider density was recorded in August (total 118, adults 77), and lowest in May (total 7, adults 2) (Table 1). Spider density was significantly higher in isolated plants and lower in plants in a patch ($F = 9.849$; $P = 0.026$). Sex ratio (♀:♂) varied from 1:1.5 in April, to 1:1 in May, and to 1:0.1 in September (Table 1). The dominant instar (both sexes) changed during the study. For example, instar IV in April, instar V in May, instars VI and IX in June, instars VII and IX in July, instars VIII (mature males) and IX (mature females) in August, with the onset of the reproductive season and the appearance of instar I; while in September the number of mature males (instar VIII) decreased and instars I, II, and III increased (Fig. 1).

Activity.—Throughout the study more spiders were in 'repose' than in any other activity. Foraging and feeding were more intense between July and September when their prey, flower visitors, were more abundant. The care of egg sacs and offspring also follows a similar pattern (Fig. 2).

Habitat selection.—The number of spiders on plants of *C. aconitifolius* varied spatially and temporally due to the combined effects of distance of the individual plant to the nearby

Table 1.—Abundance and sex ratio per month of *Peucetia viridans* living on *Cnidoscolus aconitifolius*.

Month	Number of spiders			Spider sex ratio ♀ : ♂	Number of plants sampled	Spider density per plant			Number of spiders per plant aggregation	
	Immature	Adult	Total			Immature	Adult	Total	Isolated	Grouped
April	13	5	18	1:1.5	95	0.14	0.05	0.19	16	2
May	5	2	7	1:1	181	0.03	0.01	0.04	5	2
June	20	13	33	1:0.6	178	0.11	0.07	0.19	19	14
July	34	39	73	1:0.4	183	0.19	0.21	0.40	48	25
August	41	77	118	1:0.6	183	0.22	0.42	0.64	61	56
September	31	34	65	1:0.1	183	0.17	0.19	0.36	36	26

forest, monthly precipitation, plant height, and number of panicles in anthesis. The generalized linear model fitted explained 9.59% of the variation (Table 2). Spider abundance was significantly and positively associated with plant height (χ^2 = 23.07, *df* = 1; *P* < 0.01; 1.98% of total variance). On the other hand, spider abundance was significantly and negatively correlated to distance to the nearby forest (χ^2 = −43.53, *df* = 1; *P* < 0.01; 3.73% of the total variance), monthly precipitation (χ^2 = −23.35, *df* = 1; *P* < 0.01; 2.17% of total variance), and the number of panicles in bloom (χ^2 = −9.72, *df* = 1; *P* < 0.01; 0.83% of total variance). The interaction between distance to nearby forest and precipitation was also positively correlated with spider abundance (χ^2 = 6.28, *df* = 1; *P* < 0.01; 0.54% of total variance); at the onset of the rainy season spiders were found near the forest, and as precipitation increased, the distance to the forest at which spiders were found also increased. We also found a positive significant correlation between the interaction of precipitation × number of panicles in bloom, and spider abundance (χ^2 = 3.98, *df* = 1; *P* < 0.01; 0.34% of total variance).

Forty-eight percent of the spiders were found living on plants with a range of 20–30 panicles in anthesis; which only represents 2% of the *C. aconitifolius* population. Most of the spiders were found either below or above leaves. We did not find significant differences among spider location sites on the plant, except for below and above leaves compared with those less used sites (i.e., fruits and panicles, *F* = 4.613; *P* < 0.01). Likewise, most developmental stadia did not show structure preferences. Instar IX (adult females) differed

significantly from the other instars (*F* = 2.166; *P* = 0.044) because quite frequently they were found living below the leaves. There were no significant differences in the distribution of most instars respective to plant height because most spiders were found between 60–80 cm. Again, only the location of instar IX was statistically different from the rest (*F* = 7.519; *P* < 0.001), usually nesting at heights between 1–2 m.

Synchrony between phenologies.—The number of flower visitors, the number of panicles in anthesis, the number of spiders, and the precipitation data per month are presented in Fig. 3. Grouped plants had significantly more floral visitors than isolated plants, and peak visitation was in July; we did not find differences in number of visitors among plant individuals either isolated or in groups (Table 3). There is a clear displacement in time among the peaks of blooming panicles (May), floral visitors (July), spiders (August), and precipitation (May and September). Positive significant correlations were found between the number of spiders and the abundance of floral visitors when the data was compared with one month time lag (*r* = 0.891, Pearson $(r_s)_{0.05(2),6}$ = 0.755, *P* = 0.042), and between the number of spiders and the number of panicles in bloom when the data was compared with two months time lag (*r* = 0.93, Pearson $(r_s)_{0.05(2),6}$ = 0.811, *P* < 0.05). When the abundance of spiders, floral visitors and number of panicles in bloom were correlated to monthly precipitation, we found a positive significant correlation for spider abundance when the data was compared with three months time lag (*r* = 0.949, Pearson $(r_s)_{0.05(2),6}$ = 0.77, *P* < 0.05), a negative significant correlation for
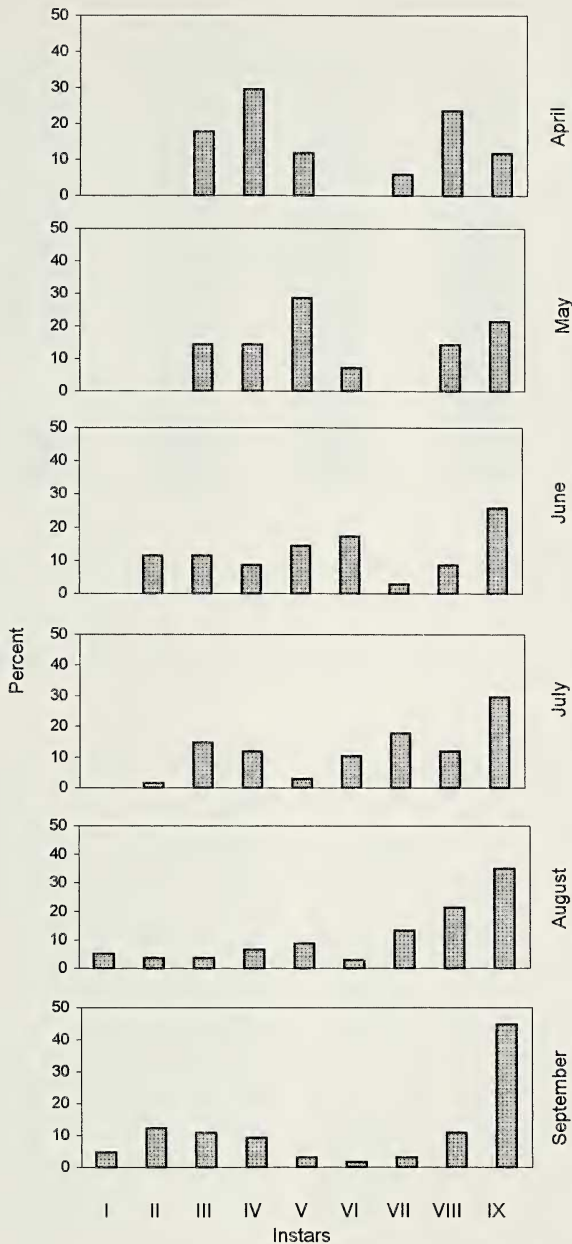
Figure 1.—Instar distribution of the population of *Peucetia viridans* through the year in Mérida, Yucatán, México. Instars I to VIII correspond to males and females, instar IX only adult females (see text, sampling design).

floral visitors when the data was compared with two months time lag ($r = -0.775$, Pearson $(r_s)_{0.05(2),6} = 0.77$, $P < 0.05$), and a non-significant correlation for the number of panicles in bloom ($r = 0.042$, Pearson $(r_s)_{0.05(2),6} = 0.77$, $P > 0.05$), although both peaked in May.

DISCUSSION

The life cycle of *Peucetia viridans* has been reported (Florida, Texas and Baja California) to start with the mating season in July, eggs are laid in September, hatching and dispersal between November and early January, and growth from January to June, when males and
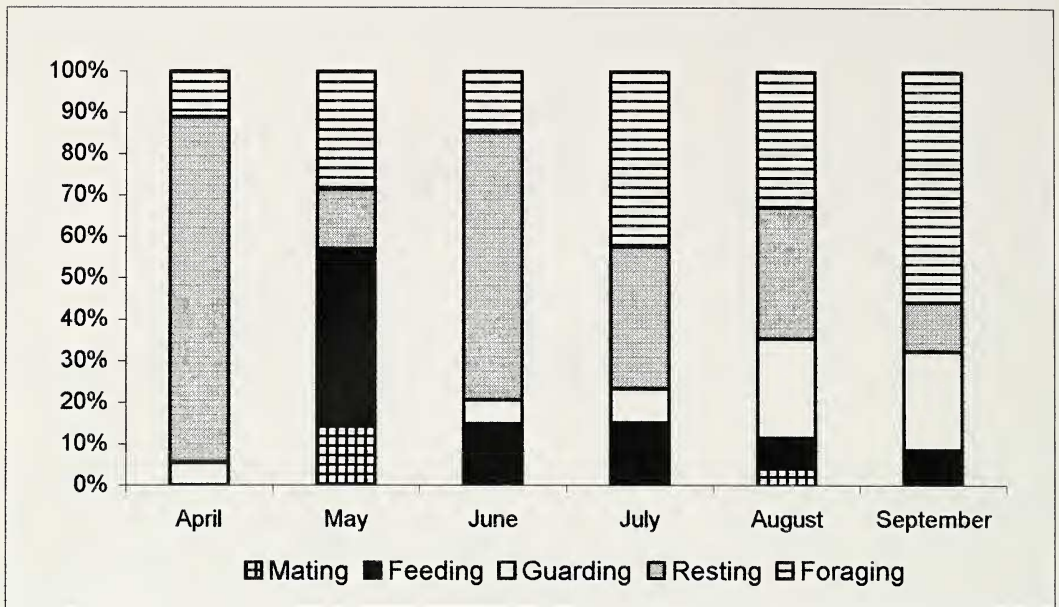
Figure 2.—Frequency of the different activities recorded for *Peucetia viridans* inhabiting *Cnidoscolus aconitifolius* in Mérida, Yucatán, México.

females reach their mature state (Brady 1964; Whitcomb & Eason 1966; Louda 1982; Van Niekerk & Dippenaar-Schoeman 1994). In Yucatán the cycle is similar, although displaced two months due to differences in the climatic patterns between our study site and the areas where the latter studies were accomplished. In Yucatán, the abundance of *P. viridans* increases when precipitation increases and temperature decreases, courtship and mating start in May, and mating peaks between June and August. One female was found guarding an egg sac in April, none were recorded in May, while this activity increased through August (26 females guarding egg sacs and progeny); finally, hatching and dispersal occurred between August and September. Feeding behavior increased in May which coincides with the pre-mating season, pre-adult maturation and growth of juveniles. Foraging behavior was well represented throughout, except for April and June. In summary, despite localities and changes in weather patterns, it seems that the phenology of the spider closely follows the changes in the physical environment of each site.

Louda (1982) found that *P. viridans* was associated with the larger individuals of *Haplopappus venetus* (Asteraceae) rather than on younger plants or on those with taller inflorescences. Our population of *C. aconitifolius* differed in the number of panicles in bloom

Table 2.—Summary of results from the generalized linear models fitted to the data on plant physical characteristics, distribution pattern, and number of spiders present.

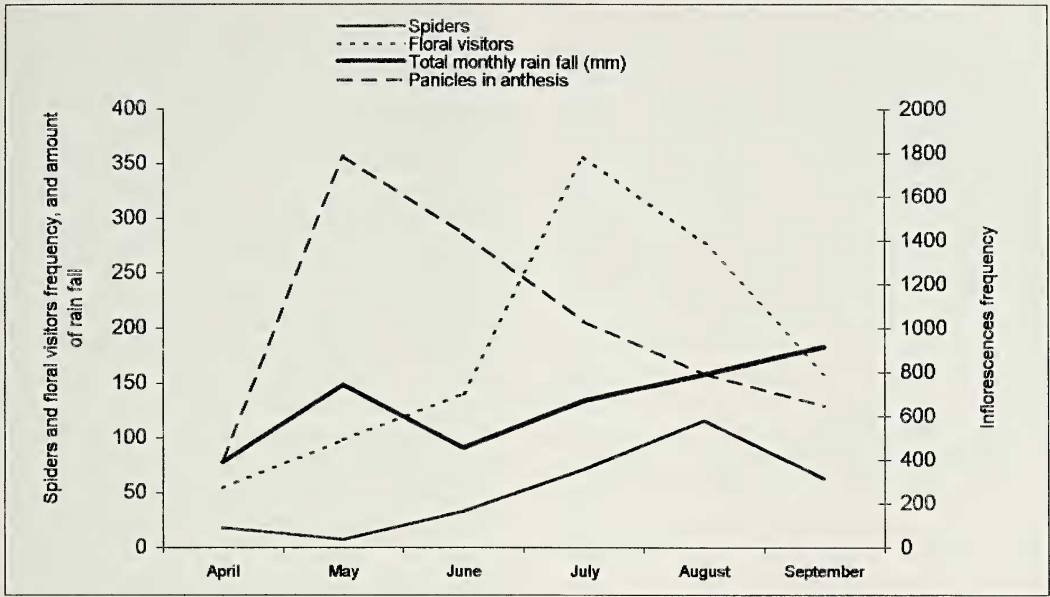| Source of variation	χ^2	df	% of variation	P
Distance to forest (A)	−43.53	1	3.73	<0.01
Precipitation per month (B)	−25.35	1	2.17	<0.01
Plant height	23.07	1	1.98	<0.01
Panicles in anthesis (C)	−9.72	1	0.83	<0.01
A * B	6.28	1	0.54	<0.01
B * C	3.98	1	0.34	<0.01
Error	1051.87	1	90.38	
Total	1163.8		100	

Figure 3.—Abundance of *Peucetia viridans*, number of panicles in bloom of *Cnidoscolus aconitifolius*, floral visitors and precipitation per month at the study site.

per plant, and more spiders were found on taller plants, with more panicles in bloom, more cover, and closer to the nearby forest patch. Sixty-five percent of the plants had between 0–5 panicles in bloom, but only 2% of the spiders were found on these plants, whereas 48% of the spiders inhabited plants with 20–30 panicles in bloom. We suggest that this pattern could be the result of the dispersal behavior (ballooning) of the spiderlings of *P. viridans*, who may take refuge in the nearby forest patch during the first months of their development, and then move back to *C. aconitifolius* individuals. Morse (1993) has proved that spiderlings may balloon more than once, increasing their probability of placement on a satisfactory hunting site. *Peucetia viridans* could be selecting larger plants (i.e., with more panicles in bloom) which will attract more floral visitors and where the spider will gain protection from the extended plant cover;

while they may select isolated plants in order to avoid or decrease competition for space. Crab spiders rely heavily on cues from the environment, such as the quantity of nectar in a flower, or the number of flowers present (Morse & Fritz 1982). We suggest that *P. viridans*, guided by color recognition and/or the amount of floral nectar, chooses plants based on the number of panicles in bloom, which increases the number of visitors, and thus spider survivorship. Morse (1991) demonstrated that *Misumena vatia* actively chooses its territory, moving from poor to high quality inflorescences. Crab spiders do not seem to respond to unopened flowers or to the number of nectar-secreting flowers, instead, they direct their response to the number of insects attracted to plants (Morse 1988). Our results suggest that *P. viridans* is selecting plants based mainly on the number of panicles in bloom and plant height.

Table 3.—Summary of the results of the three-way ANOVA comparing the abundance of floral visitors per month, visiting isolated and grouped plants.

Source of variation	df	MS	F	P
Date (month)	5	16.43	11.60	< 0.001
Plants (grouped/isolated)	1	99.81	70.51	< 0.001
Differences among plants	4	0.940	0.664	= 0.624

We expected to find an association between spider age and their vertical distribution on the plant, since adult females were found living and foraging on taller branches and inflorescences, and juveniles (3rd and 4th instars) on lower locations. However, with the exception of adult females who sought high places to lay their egg sacs, the rest of the developmental stages did not show a preferred nesting or foraging height. We did not find either any preference for location on the plant among instars. Most of the spiders were found above (34%) or below (37%) leaves, and only 15% of the spiders were found on inflorescences; but there was no preference by instar or time of year. Morse (1993) found that crab spiders choose specific leaf areas to build their nests, particularly close to favorable spiderling hunting sites. Gravid females of *P. viridans* choose the more shaded plants nearest to the forest patch, decreasing the probability of spiderling desiccation and increasing the potential food resources (more panicles in bloom). Crab spiders are very efficient in choosing the umbel with the largest number of white flowers, and the fact that their presence resembled the frequency with which insects visited umbels, rather than the number of flowers visited on these umbels, suggests that the mere appearance of an insect, however fleeting, provides the spider with the single largest amount of information required to make a choice (Morse & Fritz 1982). Thus the frequency of spider attack on their prey should provide us with useful information on site quality (Morse & Fritz 1982).

Louda (1982) found in Baja California that flowering was correlated with the relative abundance of spiders and floral visitors. In Yucatán the flowering peak occurred in May, the peak of flower visitors in June, and the peak of spider abundance in August. However, the resulting significant correlations (either with one, two or three months of time lag) among the above variables, suggest that organisms need time to respond to changes in their environment. The latter could also be an escape strategy of the plant, since blooming panicles are available to pollinators when the abundance of *P. viridans* is low.

Not all individuals of *C. aconitifolius* were inhabited by *P. viridans*. Interestingly, these were visited by geometer caterpillars which heavily damage leaves (Parra-Tabla & Car-bajal-Rodríguez, unpubl. data). Freitas & Oliveira (1996) have demonstrated that butterflies visually recognize potential egg predators, such as ants, and actively choose sites that are better for egg-laying, thereby reducing the risk of death of their offspring. It is quite possible that the geometer moths ovipositing on *C. aconitifolius* recognize *P. viridans* and thus only oviposit on those plants without spiders. Even though spiders prey heavily on the plant's pollinators, they may also impede oviposition by the moth on the plant and thereby reduce potential leaf damage, benefiting the plant (see also Louda 1982).

Finally, our results suggest that *Peucetia viridans* uses high-quality portions of its habitat, choosing those plants offering better sources of food, shelter, and favorable environmental conditions. The study of tritrophic-level interactions (e.g., plant-herbivores and/or pollinators-predators, such as spiders) should be pursued because they may yield more information on how different clustering of relationships between species affect the ecology and evolution of interactions (Price et al. 1980; Thompson 1994).

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